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The Species of *Hapalomys* (Rodentia, Muridae)

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ABSTRACT

Rats of the genus *Hapalomys* are adapted for arboreal life and live in the forests of Southeast Asia. Current published opinions regarding taxonomy of *Hapalomys* claim there is only one polytypic species in the genus, but analysis of available samples indicates there are really two distinct species: *H. longicaudatus* Blyth, which is monotypic, and *H. delacouri* Thomas, containing three subspecies. The species limits are defined on the basis of external, cranial, and dental features as well as geographic distribution.

Rats of the genus *Hapalomys* have been known to naturalists since 1859 when it was first described by Edward Blyth, a description based on specimens obtained from southern Burma. In addition to Burma, species in the genus occur in Thailand, Malaya, South Vietnam, Laos, and the island of Hainan, off the coast of southern China.

Rats in *Hapalomys* are handsome, arboreal animals (figs. 1, 2). Their upper parts are either grayish brown or ochraceous brown, their underparts are whitish. Their pelage is soft and dense, and the tail is longer than the head and body, ending in a tuft of hairs. The ears are conspicuously fringed with long vibrissae. Females have four pairs of mammae, one pectoral, one postaxillary, and two inguinal. Front and hind feet are short with long and widely spaced digits. The ventral surfaces of the digits are corrugated with narrow transverse ridges and end in large and swollen toe pads. Large pads also occupy most of the palmar and plantar

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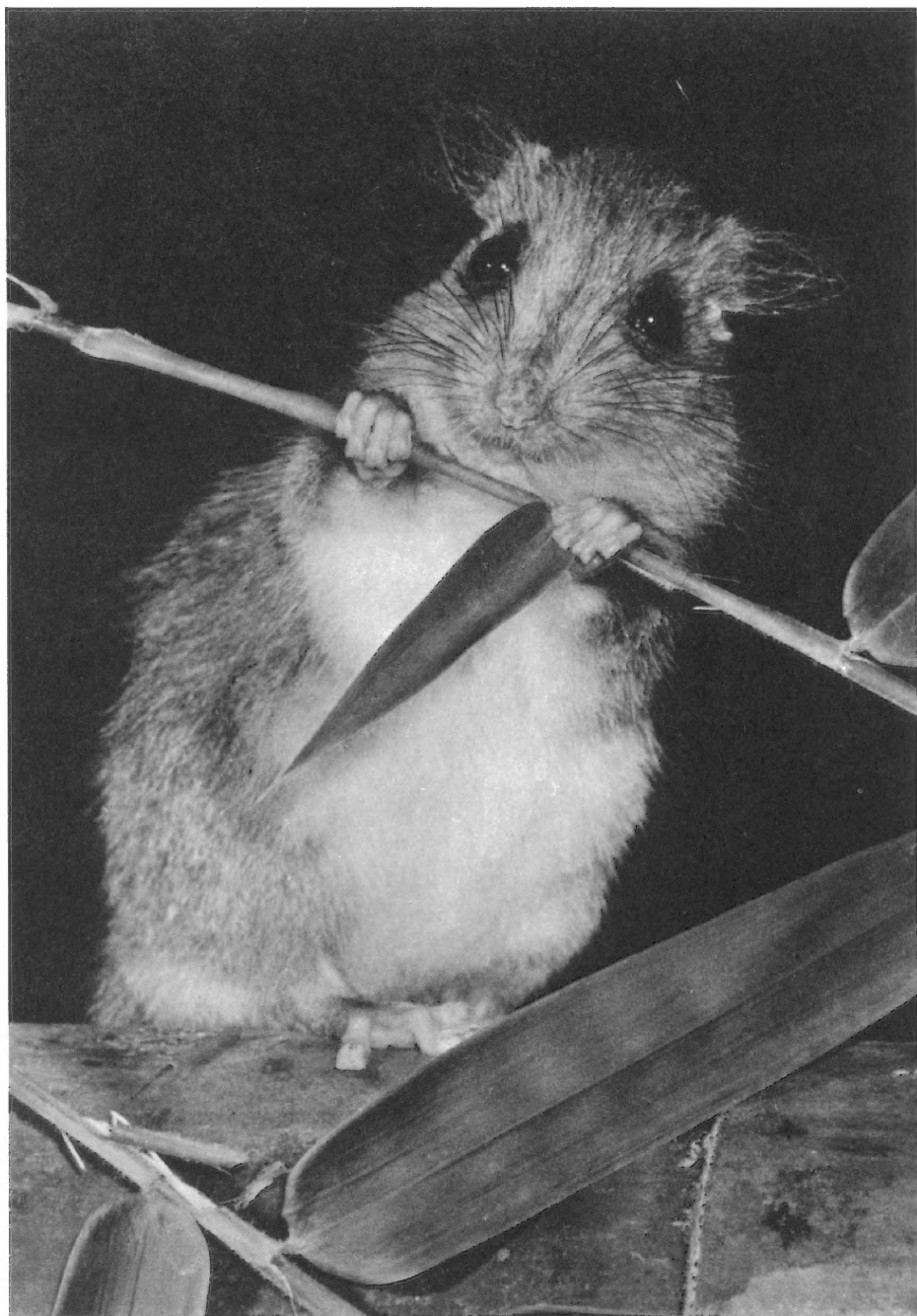


FIG. 1. *Hapalomys longicaudatus*. Young male from Blatop Valley, ulu Kelantan, Malaya. Photographed by Jane Burton.



FIG. 2. *Hapalomys longicaudatus*. Young male from Blatop Valley, ulu Kelantan, Malaya. Photographed by Jane Burton.

surfaces of each foot. The hallux is wide, fully opposable, and bears a nail rather than a claw. The animals are excellent climbers; Medway (1964) has described how they grasp terminal branches and twigs of bamboo and how they move over the larger stems.

The skull is squarish and compact, with a short, broad, and chunky rostrum. The brain case is wide and margined with prominent ridges. The incisors are wide and strong. In number and configuration of cusps the molars are unique among murids.

The morphological features of the genus were carefully described by Sclater (1890) and in less detail by others (Blanford, 1888-1891; Thomas, 1927; Allen, 1940; Ellerman, 1941, 1961; Medway, 1964, 1969). In combination of characters, the genus has invariably been regarded as unique in morphological specializations among the many species of murids known to occur in Southeast Asia. There has, however, been no agreement about the number of species within the genus. Four different names have been applied to different samples of *Hapalomys*, and these taxa have been variously interpreted as representing from one to four species. Since 1941 most workers have accepted the results of Ellerman's study; he considered all the named forms to represent one polytypic species.

My purpose here is to clarify the number of species in *Hapalomys*. The material beyond, presented primarily in tables and illustrations, documents the morphological limits of the species in this interesting genus of Asian rats.

ABBREVIATIONS AND METHODS

The specimens discussed in the present paper are in the following collections:

AMNH, the American Museum of Natural History, New York

BM, British Museum (Natural History), London

FMNH, Field Museum of Natural History, Chicago

MCZ, Museum of Comparative Zoology at Harvard College, Cambridge

MNHN, Muséum National d'Histoire Naturelle, Paris

NMS, National Museum (formerly Raffles Museum), Singapore

Measurements of head and body length, tail length, and length of ear are those of the collectors and were taken from labels attached to study skins. I measured the hind foot length (including the claw) of all specimens. Cranial measurements were taken with dial calipers graduated to tenths of millimeters. The limits of most of these measurements are explained elsewhere (Musser, 1970). The greatest length and the greatest breadth of each molar was measured with calipers under a dissecting microscope.

THE PROBLEM

The genus *Hapalomys* and the species *H. longicaudatus* were named and described in 1859 by Edward Blyth. Blyth had three specimens of this new rat and commented that "an adult male and female, with a young one were forwarded by Major Berdmore." Berdmore's specimens came from "Schwe Gyen, in the valley of the Sitang river, Tenasserim provinces" (Blyth, 1859, p. 293). Blyth did not designate a holotype. The specimens were deposited in the Indian Museum at Calcutta.

Blyth's description of *H. longicaudatus* was short, general, and poor. He failed to detail some of the most distinctive morphological features of the animal. *Hapalomys longicaudatus* was not adequately described until 31 years after Blyth's original description. Sclater (1890) redescribed and illustrated the species providing the first accurate details of the external, cranial, and dental features of *H. longicaudatus*, and that description is still one of the best available. Sclater also compared the dental topography of *Hapalomys* with *Chiropodomys* and *Vandeleuria* and offered some enticing remarks on the evolution of murine molars. Sclater's description of *H. longicaudatus* was based on a skin and an alcoholic specimen from which the cranium and mandibles had been extracted. The cranium, left mandible, upper and lower toothrows, and ventral surfaces of the front and hind feet were illustrated. All are natural size, clear, and accurate. The specimen Sclater figured and measured was from the type series collected by Major Berdmore.

One year later, Sclater (1891, p. 82) provided literature references, known geographic distribution, and listed the three known specimens for *Hapalomys longicaudatus*. Specimens "a" and "b" (a male and female, respectively) were from Sitang Valley, Burma. Both were obtained by Major Berdmore, and Sclater indicated that both specimens comprised the types of *H. longicaudatus*. Specimen "a" was indicated as a skin, and specimen "b" as an alcoholic with skull. The third specimen was designated specimen "c," an alcoholic female from Mita, Tavoy, Burma. It was obtained by a "Museum Collector." The two type specimens from the Sitang Valley are in the Indian Museum at Calcutta. I have not had an opportunity to examine them. The specimen from Mita, however, is now in the British Museum (Natural History) and I was able to study it there in 1969.

The three other taxa in the genus *Hapalomys* were originally described as separate species. Two of them, *Hapalomys delacouri* and *H. pasquieri*, were named and described by Oldfield Thomas (1927). The other taxon, *H. marmosa*, was named and described by Glover M. Allen (1927).

These three forms have one trait in common; all are represented by small animals, half the size of *Hapalomys longicaudatus*. Thomas regarded the two species he described as distinctive and remarked that (1927, p. 57) "As a species *H. delacouri* is at once distinguishable from *H. longicaudatus* by its much smaller size, and this distinction is carried still further in the next animal (*H. pasquieri*) which is, again, a further diminutive of the same type—the three species, all very like in general characters, representing three widely separated size-stages."

From 1927 to 1940, *H. delacouri* was regarded as a distinct species of *Hapalomys*. For example, Wilfred H. Osgood (1932) reported a specimen of *Hapalomys* from Phong Saly (northern Laos) and assigned it to the taxon, *pasquieri*. Osgood considered *pasquieri* to be a subspecies of *H. delacouri*. He also pointed out that Allen's "*H. marmosa* from Hainan, of which the cranial characters are unknown, doubtless is closely allied (to *H. delacouri*)." In 1940, Allen (p. 1054) regarded *marmosa* to be a subspecies of *H. delacouri*.

John R. Ellerman (1941) considered all the named forms of *Hapalomys* to belong to one species. Ellerman had examined representatives of *delacouri*, *longicaudatus*, and *pasquieri*. He noted (1941, p. 81) that *pasquieri*, "based on a very young specimen with all the molars not fully cut yet, is best regarded as a synonym of *delacouri*. I do not think there is more than a racial difference between any of the forms examined; I have not seen the Hainan form." In volume three, Ellerman (1949, p. 27) mentioned that "G. M. Allen makes his Hainan form *marmosa* a race of *delacouri*, which I think may stand as a well-marked race of *longicaudatus*."

Ellerman's view that there was only one species in *Hapalomys* has been accepted from 1941 to the present (Ellerman and Morrison-Scott, 1951; Ellerman, 1961), with the exception of Misonne (1969) who suggested that *H. delacouri* may be a distinct species. Ellerman's taxonomic opinion of the contents of *Hapalomys* has not generally been questioned because there are so few specimens of *Hapalomys* in museum collections, and apparently few persons have carefully re-examined the type material. In 1969 I had the opportunity to study all but one of the holotypes and most available specimens of all named forms that are in museum collections. The material consists primarily of study skins and skulls. Results of my study indicate that there are two distinct species of *Hapalomys*: *H. longicaudatus*, which is monotypic, and *H. delacouri*, with the subspecies *H. d. pasquieri* and *H. d. marmosa*. The evidence for this conclusion is presented below.

COMPARISONS BETWEEN *HAPALOMYS LONGICAUDATUS* AND *HAPALOMYS DELACOURI*

The two species of *Hapalomys* differ conspicuously in external features

TABLE 1

DISTINGUISHING EXTERNAL FEATURES OF *Hapalomys longicaudatus* AND *Hapalomys delacouri*
(Comparisons are based on study skins of adults.)

Feature	<i>H. longicaudatus</i>	<i>H. delacouri</i>
Upper parts	Grayish brown; pelage thick and soft, woolly; upper parts separated from underparts by ochraceous strip	Ochraceous brown; pelage thick, softer, silky rather than woolly; no strip between upper parts and underparts
Underparts	White; pale ochraceous suffusion on axillary, inguinal, and abdominal areas of some specimens	Dead white; no ochraceous suffusion
Face	Dark, grayish brown; including area above lips, beneath whiskers, and on cheeks	Ochraceous brown; white of underparts extends above the lips on either side of rhinarium, beneath whiskers, and onto cheeks
Ear	Small relative to size of head and body (fig. 6); dark brown; black auricular vibrissae	Same absolute size, thus significantly larger relative to size of head and body; brown ears and auricular vibrissae
Tail	Long (table 2); well haired on distal third (fig. 3)	Absolutely shorter and shorter relative to length of head and body; distal third scantily haired
Feet	Large (table 2, figs. 4 and 5)	Miniature of the feet of <i>H. longicaudatus</i>

(table 1) and in actual and relative size (tables 2, 3, fig. 6). *Hapalomys longicaudatus* is a large animal with brownish gray upper parts and whitish underparts. It is about the size and bulk of a young adult house rat, *Rattus rattus*. *Hapalomys delacouri* is half the size and bulk of *H. longicaudatus*. It resembles *Chiropodomys gliroides* in external features but is larger. In addition to size, *H. delacouri* differs conspicuously from *H. longicaudatus* in coloration of upper parts and underparts, color and markings of face, relative size of the ear, and pilosity of the tail (table 1).

Proportional relationships between samples of the two species are graphically illustrated in the form of a ratio diagram in figure 6. Simpson (1941) described the method for constructing ratio diagrams but figure 6 requires a brief explanation. For each measurement, the absolute value of the mean and the absolute values of plus and minus two standard errors of the mean were converted to logarithms. The sample of *H. longicaudatus*

TABLE 2

EXTERNAL MEASUREMENTS (IN MILLIMETERS) FROM SPECIMENS OF *Hapalomys longicaudatus* AND *Hapalomys delacouri*
(The mean, size of sample in parentheses, and observed range are listed in that order.)

	<i>H. longicaudatus</i>		<i>H.d. delacouri</i>		<i>H.d. pasquieri</i>	
	Adults ^a	Young Adult ^b	Adults ^c	Young Adult ^d	Adult ^e	Young Adult ^f Juvenile ^g
Length of:						
head and body	163.5(4) 162-165	147.5(2) 140-155	131.0(5) 123-136	115 —	121 —	102 — 91
tail	198.3(4) 193-202	185.5(2) 176-195	149.2(5) 140-160	140 —	171 —	135 — 103
hind foot	30.0(4) 28-32	29.0(2) 28-30	23.2(5) 22-24	23 —	22 —	22 — 20
ear	13.8(4) 13-15	12.0(2) 12-12	14.3(4) 14-15	— 10	— 15	— 13 14

^a BM 63.1160, 63.1162 to 63.1164. ^b BM 63.1159 and 63.1161. ^c BM 26.10.4.182 and 26.10.4.183; MNHN 1929-317 to 1929-319. ^d BM 26.10.4.184. ^e FMNH 32463. ^f MCZ 38234. ^g BM 26.10.4.185.

(from the Cameron Highlands, Malaya) was chosen as the standard. For each dimension, the logarithm of the mean of the standard was subtracted from the logarithm of the mean, and from the logarithms of plus and minus two standard errors of the mean, of the sample of *H. delacouri* (from Dakto, South Vietnam). Measurements larger than the standard are represented on the diagram by positive values, those smaller than the standard are represented by negative values. In the samples, the lines connect the means of each measurement, the horizontal bars and rectangles represent plus and minus two standard errors of the mean. A sample with all the same proportions as the standard would be represented by means on a line parallel to that of the standard, regardless of absolute size. Also, if values for the samples being compared with the standard are similar in absolute size they will be close together on the diagram. And, if proportions between any of the measured dimensions are similar, the relative positions of their points to each other on the horizontal scale will be similar.

Crania and mandibles of *Hapalomys longicaudatus* and *H. delacouri* are illustrated in figures 7–9. Proportional differences and similarities are shown in figure 6. In general configuration the skull of *H. delacouri* is a miniature version of the skull of *H. longicaudatus*. There are, however, conspicuous qualitative and proportional cranial differences between the two species. In addition to the difference in size, the cranium of *H. delacouri* differs conspicuously from that of *H. longicaudatus* in relative sizes of the nasals and rostrum and in significantly longer incisive foramina relative to greatest length of the skull. The rostrum of *H. delacouri* is long, slender, and delicate compared with the short, wide, and robust rostrum of *H. longicaudatus*. *Hapalomys delacouri* has a wide and shallow braincase; it is much wider relative to its depth than in *H. longicaudatus*. In *H. delacouri* the anterior edge of each zygomatic plate does not project beyond the dorsal maxillary root of each zygomatic arch. In dorsal view the zygomatic notch is usually missing in *H. delacouri*; when present it is very shallow, never deeper than 0.5 mm. in the specimens at hand. In contrast, the anterior edge of each zygomatic plate of *H. longicaudatus* projects beyond the dorsal maxillary root of each zygomatic arch and the zygomatic notch is conspicuous when the skull is viewed from above. The depth of the notch ranges from 1.0 to 1.3 mm. in adults available to me for study.

There are also proportional differences between the two species in certain dimensions of breadth on the ventral surfaces of the skulls. For example, in *H. delacouri* the breadths of the palatal bridge, incisive foramina, and mesopterygoid fossa are significantly wider relative to most

TABLE 3

CRANIAL MEASUREMENTS (IN MILLIMETERS) FROM THE SPECIMENS OF *Hapalomys longicaudatus* AND *Hapalomys delacouri* LISTED IN TABLE 2
(The mean, size of sample in parentheses, and observed range are listed in that order.)

	<i>H. longicaudatus</i>		<i>H. d. delacouri</i>		<i>H. d. pasquieri</i>	
Greatest length of skull	40.47(3) 39.7-41.5	38.00(2) 37.9-38.1	34.00(3) 33.6-34.2	31.9 —	32.0 —	29.5 —
Zygomatic breadth	21.63(3) 21.3-22.0	20.15(2) 20.0-20.3	17.57(3) 17.4-17.8	16.8 —	17.5 —	16.0 —
Interorbital breadth	5.83(4) 5.7-6.0	5.45(2) 5.4-5.5	4.75(4) 4.3-5.1	4.4 —	4.7 —	4.0 —
Length of nasals	12.25(4) 11.5-12.6	12.05(2) 12.0-12.1	11.87(3) 11.7-12.0	10.7 —	10.5 —	9.3 —
Length of rostrum	9.93(4) 9.7-10.2	9.50(2) 9.4-9.6	9.47(3) 9.3-9.7	8.2 —	8.3 —	7.3 —
Breadth of rostrum	7.95(4) 7.6-8.3	7.3(2) —	6.38(4) 6.0-6.7	5.7 —	6.1 —	5.9 —
Breadth of brain case	16.70(3) 16.6-16.9	16.3(2) —	15.20(4) 15.1-15.3	14.7 —	15.3 —	14.7 —
Height of brain case	11.63(3) 11.2-12.0	11.20(2) 11.1-11.3	9.33(4) 9.1-9.5	8.9 —	9.0 —	9.2 —
Breadth across incisor tips	3.88(4) 3.6-4.0	3.50(2) 3.4-3.6	2.88(4) 2.6-3.1	2.5 —	2.6 —	2.3 —
Breadth of zygomatic plate	5.10(4) 4.7-5.4	5.15(2) 5.0-5.3	3.68(4) 3.6-3.9	3.3 —	3.6 —	3.3 —
						2.6 —

TABLE 3—(Continued)

	<i>H. longicaudatus</i>		<i>H. d. delacouri</i>		<i>H. d. pasquieri</i>	
Depth of zygomatic notch	1.18(4) 1.0–1.3	1.0(2) —	.18(4) .0–.5	.0 —	.5 —	.4 —
Length of diastema	8.45(4)	9.35(2)	8.45(4)	7.6	8.1	7.1
	9.8–10.9	9.1–9.6	8.1–8.8	—	—	—
Palatal length	20.78(4)	20.5(2)	17.48(4)	16.2	15.8	15.0
	18.1–22.3	—	16.9–18.0	—	—	—
Length of palatal foramina	6.53(3)	6.30(2)	6.28(4)	5.8	5.6	5.1
	6.2–6.8	6.2–6.4	6.1–6.6	—	—	—
Breadth of palatal foramina	1.83(3)	1.95(2)	1.95(4)	2.0	2.0	2.0
	1.7–1.9	1.9–2.0	1.9–2.0	—	—	—
Length of palatal bridge	9.50(3)	9.05(2)	6.85(4)	6.5	6.0	6.3
	9.4–9.6	8.9–9.2	6.4–7.1	—	—	—
Breadth of palatal bridge at M ¹	2.27(3)	2.2(2)	2.35(4)	2.3	2.6	2.5
	2.2–2.3	—	2.1–2.6	—	—	—
Breadth of mesopterygoid fossa	2.10(3)	2.2(2)	1.93(4)	1.9	1.9	1.6
	—	—	1.8–2.1	—	—	—
Length of bulla	8.37(3)	7.90(2)	6.25(4)	6.3	6.0	—
	8.2–8.5	7.8–8.0	—	—	—	—
Alveolar length of M ¹⁻³	7.93(4)	7.9(2)	6.35(4)	6.7	5.9	5.8
	9.9–8.0	—	—	—	—	—

other dimensions of the skull than in *H. longicaudatus*.

The mandibles of the two species differ primarily in size. They are illustrated in figure 9.

Upper and lower toothrows of *H. longicaudatus* and *H. delacouri* are contrasted in figures 10 and 11. Size is the primary difference between the two species. The teeth of *H. delacouri* are a miniature version of those of *H. longicaudatus* in pattern of most cusps and in proportions of lengths and



FIG. 3. Distal portions of tails of *Hapalomys longicaudatus* (left) and *H. delacouri* (right). Natural size.

breadths of each tooth. The only qualitative differences I detected involved the two small cusplets that lie on the anterior margins of each upper first molar and the size and position of the anterolingual cusp of each upper first molar. In *H. longicaudatus*, the two cusps on the anterior margin of each upper first molar, although small, are well developed and conspicuous; they are clearly shown in figure 10. In contrast, most examples of *H. delacouri* do not have these cusps. In the few specimens with cusps, they are represented by minute, inconspicuous spicules. This difference between the two species was pointed out by Thomas (1927) in his original description of *H. delacouri*.

The shape of the first upper molars is different in the two species, a reflection of the size of the lingual cusp on the anterior row of cusps of each first upper molar. In *H. delacouri* each cusp is smaller relative to sizes of the other cusps of the tooth, than in *H. longicaudatus*. As a result, the anterolingual corner of each molar appears beveled, a consistent differ-

ence between available specimens of the two species, and a difference that is clearly shown in figure 10.

Like the maxillary toothrows, the mandibular toothrows of *H. delacouri* are miniatures of the teeth of *H. longicaudatus*. The only other difference I could find involved the small cusplets on the posterior border of each lower second molar. In *H. longicaudatus* there are two small but well-developed cusplets on the posterior margin of each second molar. One cusp is directly on the posterior edge, the other is situated on the postero-labial edge of the tooth. In *H. delacouri*, only the very posterior cusplet is well developed and conspicuous. The labial cusplet is usually absent, but may be represented by a minute bump. The differences are clearly illustrated in figure 11.

GEOGRAPHIC DISTRIBUTION, SUBSPECIES, AND HABITS

Hapalomys longicaudatus

Hapalomys longicaudatus is known by a few specimens from scattered localities in southern and peninsular Burma, southwestern and peninsular Thailand, and Malaya. Specimens I have examined are listed below. The localities from which they were obtained are mapped in figure 12. I have also listed and mapped specimens and localities recorded in the literature. The number in front of each locality refers to the numbered locality on the map.

1. Schwegyin, in the valley of the Sittang River, southern Burma; the type locality (Blyth, 1859). I have not examined the type specimen, but Sclater's (1890) figures of one of the types clearly belong with the large rat, not the smaller *H. delacouri*.
2. Meta, Tavoy, peninsular Burma (BM 90.10.1.1.); an adult female that was originally in the collection of the Indian Museum at Calcutta (Sclater, 1891) but it is now at the British Museum. The date of collection is unknown.
3. Bankachon, near Victoria Point, southern tip of peninsular Burma (BM 14.12.8.147); young adult male obtained December 22, 1913, by G. C. Shortridge.
4. Me Wong River, 53 mi. E Um Pang, 250 m., southwestern Thailand (AMNH 54754); juvenile female, obtained February 23, 1924, by A. S. Vernay.
5. Quaa Noi (spelled Khwae Noi on my recent maps) River, southwestern Thailand (BM 14.5.3.1); adult female obtained January 11, 1914. This is the specimen that G. K. Gairdner recorded in 1914. He presented the specimen to the British Museum. The records in that museum indicate the specimen came from the Mae Klong River (lat. 14° 30' N, long. 98° 50' E). Gairdner (1914, p. 115) indicated that the specimen was "found in uninhabited bamboo and teak jungle on the Quaa Noi river, N. Lat. 14° 22'." The Khwae Noi River is a tributary of the Mae Klong and the coordinates cited above in parentheses place the location on the Khwae Noi, not near the Mae Klong. Shortly after this first record was published, Gairdner (1915, p. 254) reported another specimen of *H. longicaudatus* obtained from Sai Yoke District, within 3 miles of the locality



FIG. 4. Dorsal views of right hind feet (dry study skins) of *Hapalomys*. Left: *H. longicaudatus* (BM 63.1160, adult male) from ulu Kelantan, Malaya. Right: *H. delacouri* (BM 26.10.4.182, adult male) from Dakto, South Vietnam. Approximately $\times 3$.

near the Khwae Noi River where the other specimen was captured. I have not seen this specimen, but there is a study skin of *H. longicaudatus* in the British Museum (BM 15.12.1.19), a male, that was presented to the museum by Gairdner. The only data I could find regarding the rat was that it was from "S. W. Siam." As far as I know, Gairdner only obtained two specimens of *H. longicaudatus*, and this specimen could very well be the one he reported in 1915.

6. Patani (spelled Pattani on recent maps), southern tip of peninsular Thailand. I have not been able to verify this record. The specimen on which it is based was originally recorded by Hanitsch in the Report of the Raffles Library and Museum, published in 1897. I have been unable to locate this report, but in his paper Flower (1900, p. 360) referred to it.
7. Cameron Highlands, Kelantan, Malaya (BM 63.1159, young adult male; 63.1160, adult male; 63.1161, young adult female; 63.1162, adult female; 63.1163, adult female; 63.1164, young adult female). These specimens were obtained on January 19, 26, and 27, 1963. They were presented to the British

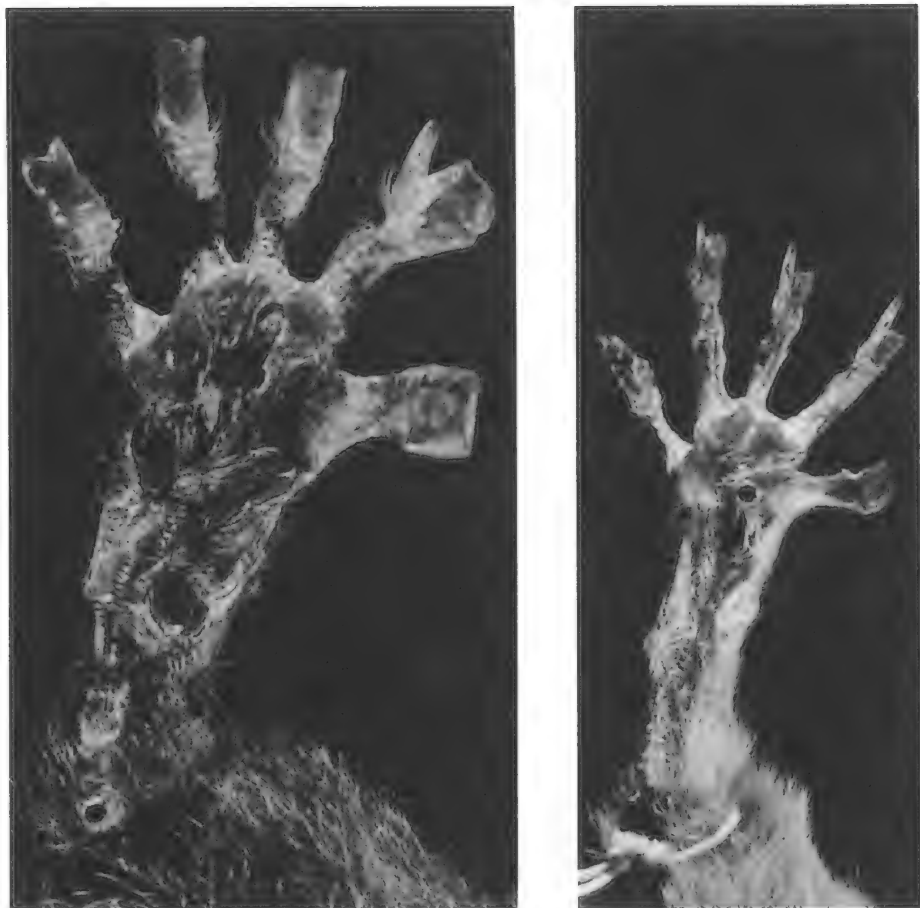


FIG. 5. Ventral views of right hind feet of same specimens of *Hapalomys* illustrated in figure 4. Approximately $\times 3$.

Museum by Lord Medway. He (1964, p. 105) reported that "All these specimens came from the vicinity of Fort Brooke, in the upper Sungei Nenggiri (at this point called the Brok), principally from the valley of the Sungei Blatop which joins the Brok at Fort Brooke." Most of the specimens were obtained from an elevation of 500 m.

8. Genting Semangko (The Gap), Pahang, Malaya (NMS 52/15); adult female obtained January 8, 1915.
9. Near Kuala Lumpur, Malaya; an adult male, collected February 10, 1949. Its skull was illustrated by Van Peenen, Ryan, and Light (1969, p. 151). The specimen is supposed to be in the collection of the National Museum of Natural History, Smithsonian Institution, but I have not been able to locate it there.

There are too few geographic localities represented by the specimens at hand and too few specimens from each place to assess the range of

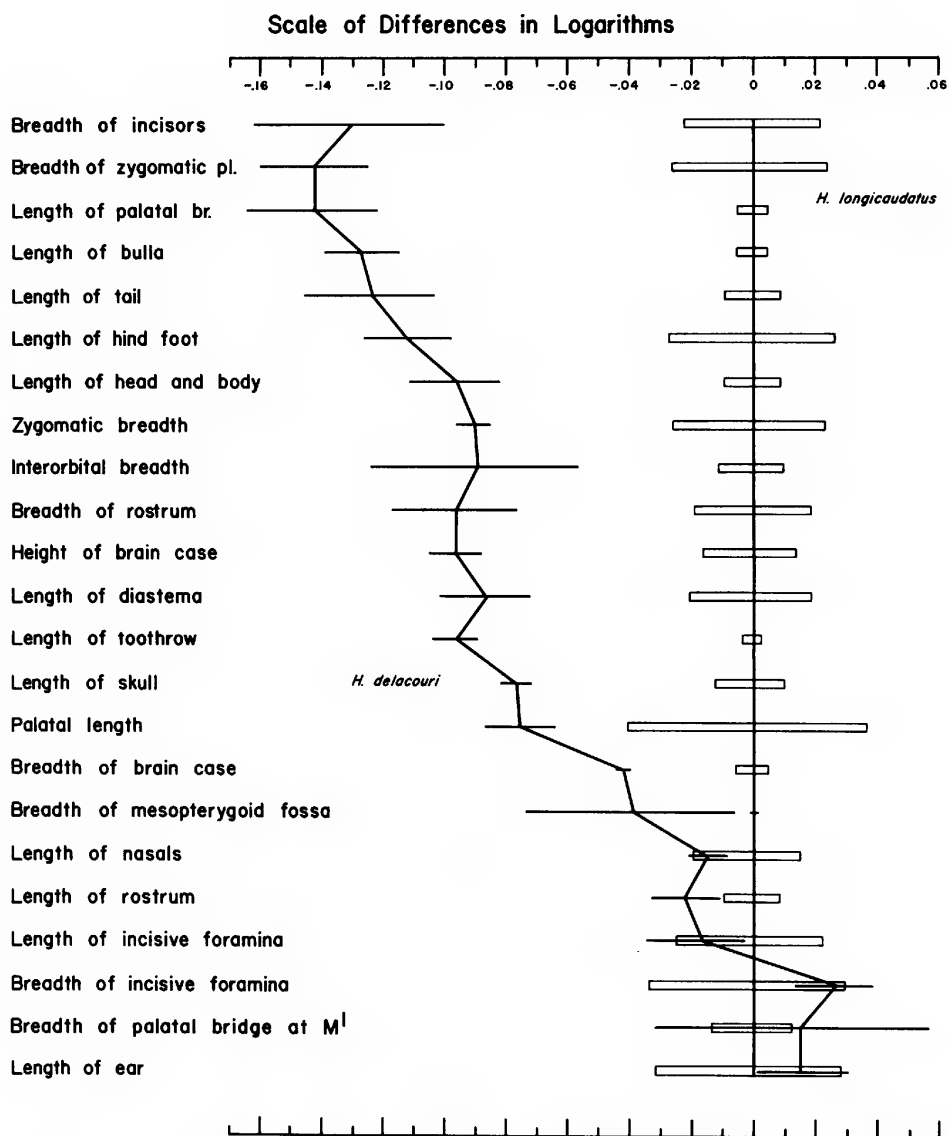


FIG. 6. Ratio diagram. Twenty-three dimensions are compared in samples of *Hapalomys longicaudatus* (the standard) from Malaya and *H. delacouri* from South Vietnam. See text for additional information.

geographic variation in external and cranial features of *H. longicaudatus*.

Aspects of the biology of *Hapalomys longicaudatus* were reported by Medway (1964). There he discussed the habitat, locomotion, diet, and ectoparasites of the population from the Cameron Highlands in Malaya. He also provided excellent photographs of the living animals and their



FIG. 7. Dorsal (left) and ventral (right) views of crania. Top: *Hapalomys longicaudatus* (BM 63.1160, adult male), ulu Kelantan, Malaya. Bottom: *H. delacouri* (MNHN 1929-317, adult male), Dakto, South Vietnam. Approximately $\times 2$.

habitat in the Blatop Valley. Medway indicated that *H. longicaudatus* was found only in association with a bamboo, *Gigantochloa scortechinii*, where the animals made nests in the larger stems. One rat that Medway had in captivity preferred the growing tips of bamboo twigs as well as fruiting twigs of bamboo. Medway implied that *H. longicaudatus* is restricted in its



FIG. 8. *Hapalomys longicaudatus*, top. *H. delacouri*, bottom. Lateral views of same specimens illustrated in figure 7. Approximately $\times 2$.

diet to various parts of the bamboo. *Chiropodomys gliroides* occurs together with *H. longicaudatus* and also frequently nests in the bamboo stems.

There is little information about the habitat in which the specimens of *H. longicaudatus* were taken in Burma and Thailand. However, they were associated with bamboo. For example, the specimen (BM 14.5.3.1.) obtained by Gairdner from the Khwae Noi River (loc. 5) was caught by persons clearing a bamboo jungle to form a camp. The only other specimen for which there is some indication of habitat is that obtained at Bankachon, near Victoria Point (loc. 3). On the label attached to the study skin is the notation that the specimen was "found among bamboos with *Chiropodomys*."

Hapalomys delacouri

I have examined 10 specimens of *H. delacouri*, obtained from the island of Hainan, northern Laos, and South Vietnam. The specimens comprise three named forms. These taxa, the specimens I examined, and their



FIG. 9. *Hapalomys longicaudatus*, left, *H. delacouri*, right. External (top) and internal (bottom) views of mandibles from same specimens illustrated in figure 7. Approximately $\times 2$.

geographic origins are listed below. The number in front of each locality refers to the numbered locality on the map in figure 12.

H. d. delacouri:

10. Dakto, South Vietnam (BM 26.10.4.182, adult male; BM 26.10.4.183, adult male, holotype; BM 26.10.4.184, young adult female; MNHN 1929-317, adult male; MNHN 1929-318, adult male; MNHN 1929-319, young adult male). These six specimens were obtained by Jean Delacour and Willoughby Lowe on March 12, 15, and 17, 1926.

H. d. pasquieri:

11. Xieng Kuang, northern Laos (BM 26.10.4.185, holotype); Juvenile male collected March 1, 1926, by J. Delacour and W. Lowe.

12. Col de Taloun, northern Laos (MCZ 38234); young adult male obtained January 28, 1939, by J. Delacour and J. Greenway.

13. Phong Saly, 1300 m., northern Laos (FMNH 32463); adult male obtained April 28, 1929, by R. W. Hendee.



FIG. 10. *Hapalomys longicaudatus*, left and *H. delacouri*, right. Occlusal views of right upper molars of same specimens shown in figure 7. Top is anterior. Approximately $\times 15$.

H. d. marmosa:

14. Near Nodoo, on the island of Hainan, off the coast of southern China (AMNH 59046, holotype); adult female obtained December 27, 1922 by Clifford Pope.

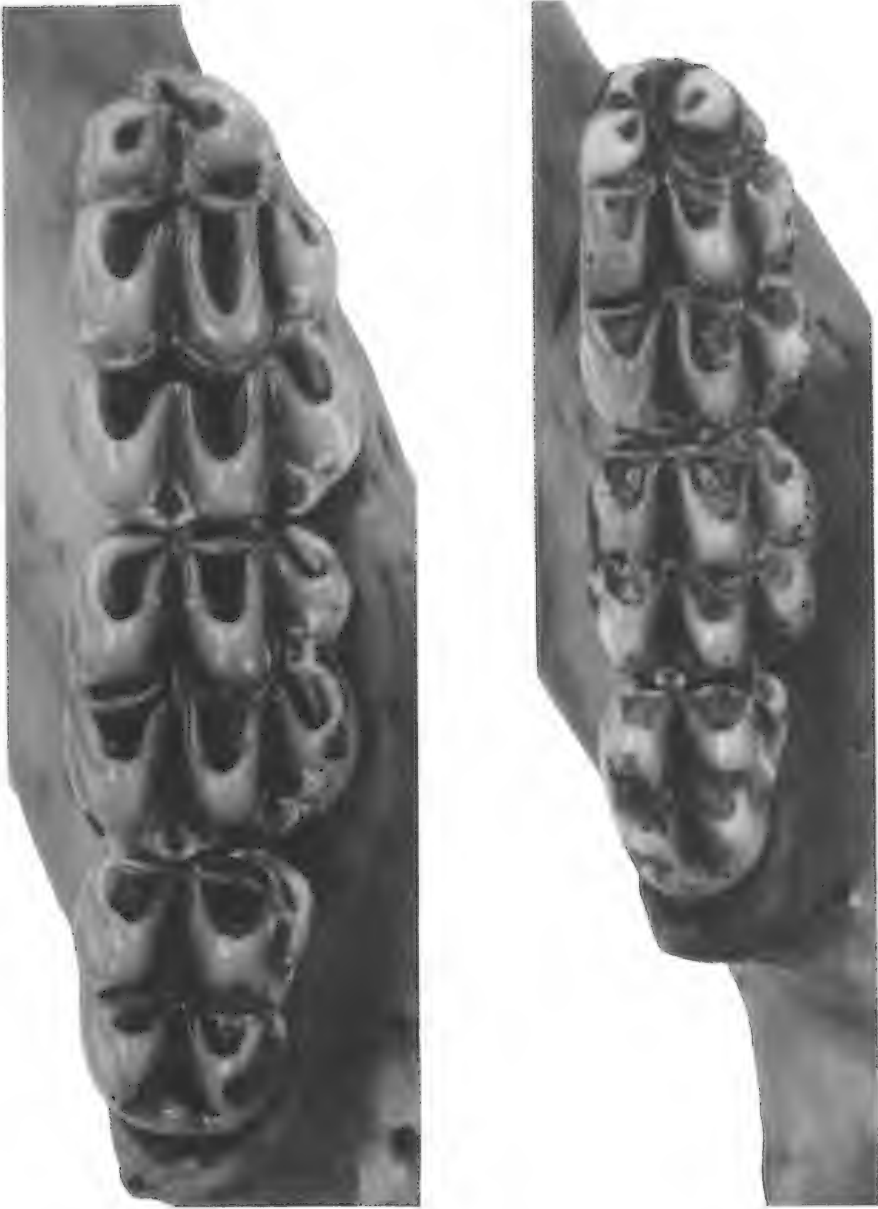


FIG. 11. *Hapalomys longicaudatus*, left, *H. delacouri*, right. Occlusal views of right lower molars of same specimens illustrated in figure 7. Top is anterior. Approximately $\times 15$.

All the specimens of *H. d. delacouri* from South Vietnam that I have examined were originally studied by Thomas (1929) and he has given a

detailed and accurate description of the species.

Judged by study of the specimens at hand, the sample of *H. delacouri* from northern Laos is a distinctive and well-differentiated population that deserves subspecific recognition (*H. d. pasquieri*) as Osgood (1932) recognized. The taxon is known from three males, an adult, young adult, and juvenile. The holotype is clearly a juvenile. Most of the sutures of its cranium are either open or only partially closed and the upper and lower third molars are partially erupted. Thomas (1927, p. 57) described *H. d. pasquieri* as a full species. He recognized that the holotype was immature and pointed out that *pasquieri* was "a more northern representative in Laos of *H. delacouri*; readily distinguishable by its smaller molars, the general characters appearing to be very much the same, so far as can be judged from a single immature example."

I cannot detect any significant differences in color of pelage between the specimens from Laos and those of *H. d. delacouri* from South Vietnam, but the two samples differ significantly in pilosity of tail and cranial and dental features. In the specimens from Laos, the distal third of each tail is covered with long hairs that extend beyond the tip where they form a dense brush 5 to 7 mm. long, a conspicuous contrast to the scantily haired tails of the specimens from South Vietnam.

The most conspicuous cranial and dental differences between the specimens from Laos and those from South Vietnam involve size and relative proportions. Most cranial dimensions of *H. d. pasquieri* are less than those of *H. d. delacouri* when adults of similar age are compared (table 3). The two adults from Laos have a noticeably shorter and more delicate rostrum than that of *H. d. delacouri*. The delicate rostrum is actually narrower and shorter and also relatively shorter in comparison with the greatest length of skull. Each specimen from Laos has a wider and shallower brain case, and this region of the skull appears flattened in comparison with skulls of *H. d. delacouri*. The molars of *H. d. pasquieri* are significantly smaller than those of *H. d. delacouri*, as is shown by the difference in alveolar lengths of maxillary toothrows (table 3); ranges of variation in the two samples do not overlap in this dimension.

Shih (1930) reported 11 specimens of *H. pasquieri* from Kutchen and Loshian, Kwangsi, China, and listed measurements of one rat from that series. Those measurements are more like examples of *Chiropodomys gliroides*. Allen (1940, p. 1054) examined one of the specimens from Shih's sample and noted that it was a *Chiropodomys gliroides*, and he cautioned that without confirmation of the identity of the other specimens the inclusion of *H. delacouri* in the Chinese fauna would be at best provisional.

Hapalomys delacouri marmosa is represented only by the holotype, an

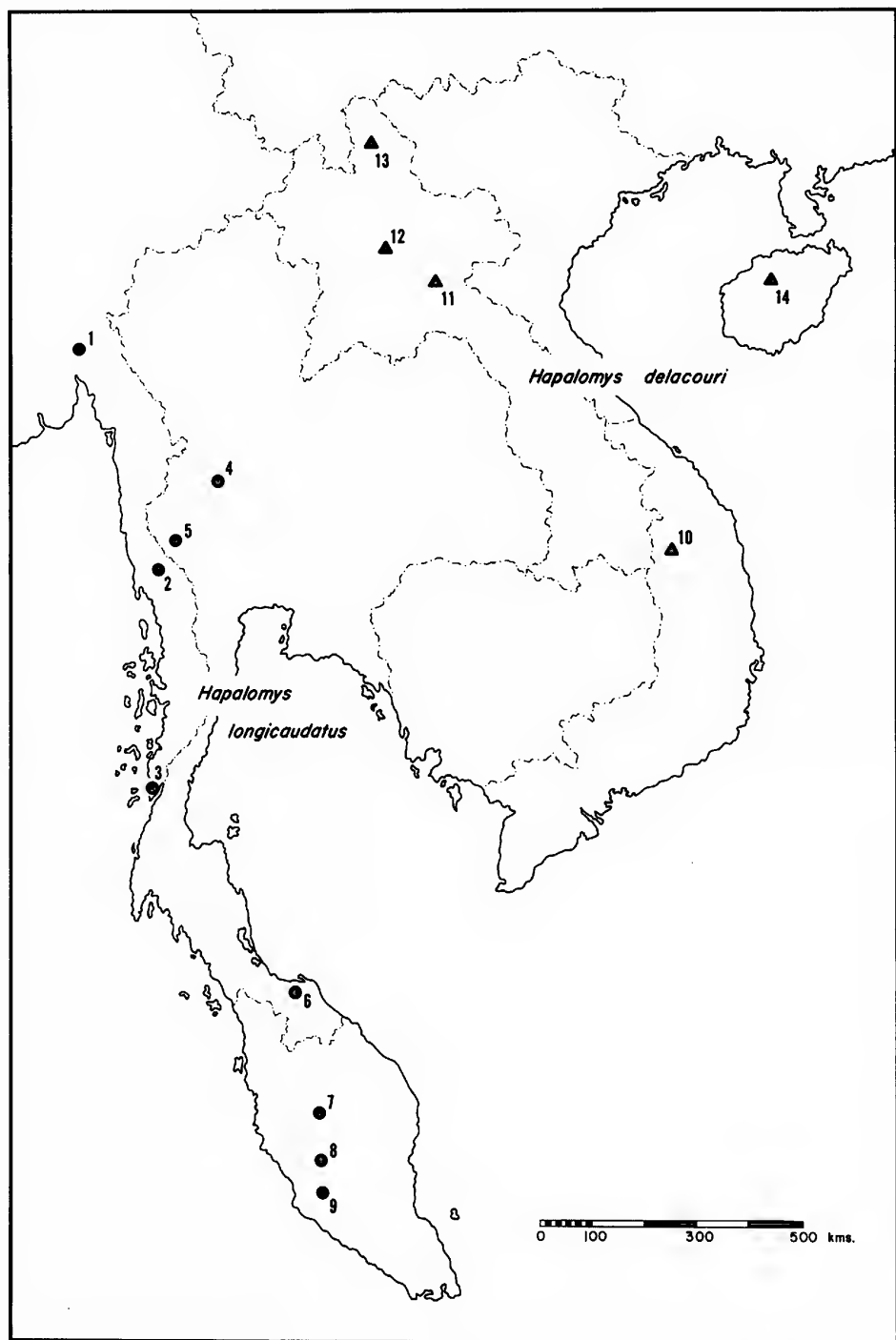


FIG. 12. Geographic distribution of *Hapalomys longicaudatus* and *H. delacouri* in Southeast Asia.

overstuffed skin without skull. External measurements are length: of head and body 130; of tail 138; of hind foot 22; and of ear 12. Allen (1927, 1940) has provided detailed and accurate descriptions of the skin, and was the first to regard *marmosa* as a subspecies of *H. delacouri*. In external dimensions and features of pelage, the specimen does not differ significantly from the sample of *H. delacouri* from South Vietnam. Whether it represents a distinctive island population, or whether it is more closely related to one of the named populations on the mainland will not be known until specimens with skulls become available.

Shih (1930) recorded a specimen of *H. delacouri* from Loshian, Yao Shan, Kwangsi, China, and commented that "The present specimen agrees with the description given by Thomas in external characters, but the teeth differs [sic] and agrees quite well with the genotype, '*longicaudatus*,' yet differs from it by the far smaller size which is very near to the dimensions given by Thomas for '*delacouri*.'" Allen (1940, p. 1055) did not have opportunity to examine this specimen, but he noted that "if it proves to be valid, will extend the known range of this tropical genus into the extreme provinces of the Chinese mainland." I have not been able to verify this possible record.

Information on habitat of *H. delacouri* is scanty and the little that is available applies only to the samples from South Vietnam and Laos; there is no information about the habitat in which the specimen from Hainan was collected. All the samples from the mainland were taken in the highlands, from elevations of 1200 to 1500 meters. Most of these specimens were obtained by J. Delacour, W. Lowe, and J. Greenway. Although general descriptions of the habitats in which these persons worked have been published (Delacour and Jabouille, 1927; Delacour, 1933; Delacour and Greenway, 1940), nothing is known about the specific microhabitat in which the specimens of *H. delacouri* were obtained.

Both Delacour and Greenway are now working at the American Museum of Natural History and they generously provided me with some additional information about the rats and the localities. Delacour recalled that all the rats from Dakto and Xieng Kuang had been obtained in wet tropical forest by native collectors. The specimen from Col de Taloun came from dry forest comprised mostly of oak and chestnut. Delacour also mentioned that the specimens had been taken above ground and that the animals were certainly arboreal. Future collectors should look for them in stands of bamboo, as well as among the vines, branches of low trees, and shrubs of the understory.

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